Ilex guaramacalensis (Aquifoliaceae), a New Species from the Ramal de Guaramacal in the Venezuelan Andes

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ABSTRACT. *Ilex guaramacalensis* Cuello & Aymard (Aquifoliaceae), a new species from the Andean forests and páramos of Guaramacal massif in Venezuela, is described and illustrated, and its morphological relationships with allied species are discussed. *Ilex guaramacalensis* is morphologically similar to *I. kunthiana* Triana from the high mountains of Costa Rica and Panama, the Coastal Cordillera, and the Andes of Venezuela to Peru, but the new species differs by the shape of its young branchlets, leaves, pedicels, and petals; the higher number of secondary veins; the shorter inflorescences; and the 4-merous flowers. Information about the floristic composition and habitat characteristics for the new species is also provided.

Resumen. Se describe e ilustra *Ilex guaramacalensis* Cuello & Aymard (Aquifoliaceae), una nueva especie de los bosques Andinos y páramos del Ramal de Guaramacal en Venezuela, y se discuten sus relaciones morfológicas con las especies afines. *Ilex guaramacalensis* es morfologicamente similar a *I. kunthiana* Triana, conocida de las montañas altas de Costa Rica y Panamá, Cordillera de la Costa y de los Andes de Venezuela hasta Perú, sin embargo, la nueva especie se diferencia por la forma de sus ramitas jóvenes, hojas, pedicelos y pétalos, el mayor numero de venas secundarias, las inflorescencias mas cortas y las flores tetrámeras. Se presenta también información sobre la composición florística y características del hábitat donde crece la nueva especie.

Key words: Andes, Aquifoliaceae, Ilex, IUCN Red List, páramo, Venezuela.

Ilex L. (Aquifoliaceae) is a genus of dioecious shrubs or trees, with simple, alternate leaves and usually 4- to 5-merous flowers that are organized in cymose inflorescences, with the cymes at times reduced to a single flower (Edwin, 1965, 1967; Loizeau & Spichiger, 1992). Comprising more than 500 species (Loizeau et al., 2007), Ilex is distributed mainly in tropical America and eastern Asia, but species have also been recorded from North America,

Europe, the Pacific islands, northeastern Australia, and sub-Saharan Africa (Loizeau et al., 2005). The first comprehensive examination of the genus was done by A. Gray (1856; see Galle, 1997), who recognized three subgenera. The German botanist Theodor Loesener later undertook a worldwide revision of the genus (Loesener, 1901, 1908, 1942). He divided the genus into five subgenera including eight series, 24 sections, and 14 subsections. Hu (1949, 1950) subsequently revised the Ilex from China based on Loesener's classification and made substantial modifications recombining infrageneric taxa and describing new series and sections. Edwin (1965) established a new section Guayanoilex, a group that has included, up to the present, all species endemic to the Guayana highlands. The genus has also been treated for floras of Cuba (González-Gutiérrez & Sierra-Calzado, 2004), Nicaragua (Hahn, 2001), Panama (Edwin, 1967; Hahn, 1993), Peru (Loizeau, 1994), Argentina (Giberti, 1979), Paraguay (Giberti, 1994), and the Flora of the Venezuelan Guayana (Steyermark & Berry, 1995). Nonetheless, recent systematic treatment of the genus is lacking. Galle (1997) published a comprehensive review of all information known about the taxonomy of the genus to date. He contested the validity of Loesener's infrageneric groups, since many of the species bear features shared by several of the subgenera, and about 50 species remain taxonomically undefined within Loesener's classification. The floral morphology is very homogeneous at an interspecific level, while leaf morphology can show great variability at this same level (Loizeau et al., 2005). Moreover, many taxa were described only with fruiting material or only with either staminate or pistillate specimens (Edwin, 1965; Steyermark, 1988). This situation has tended to overestimate the diversity of Ilex, however; for a dioecious genus like Ilex, it is always recommended to have sufficient additional material collected before describing a new species.

During the past 20 years, integrated surveys by personnel of the Herbario Universitario (PORT), Universidad Nacional Experimental de los Llanos

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Occidentales "Ezequiel Zamora" (UNELLEZ)-Guanare, in the cloud forests and páramo vegetation of the Guaramacal National Park, in the Andes of Trujillo state, Venezuela (Ortega et al., 1987; Cuello, 1999, 2000, 2002, 2004; Dorr et al., 2000), have revealed a number of new plant species to science (Morillo, 1988; Axelius & D'Arcy, 1993; Carnevali & Ramírez, 1998; Aymard et al., 1999; Taylor, 2002; Stergios & Dorr, 2003; Stančik, 2004; Niño et al., 2005). More recent vegetation surveys have uncovered a previously undescribed species of the genus *llex*. Sterile material had been collected many times in the surveys but could not be matched to any known species of Ilex. Upon the finding of fertile material (staminate and pistillate flowers and fruits), the specimens were at first determined as *llex* cf. kunthiana Triana based on its similar leaves and 1-flowered pistillate inflorescences. However, a detailed study of specimens available in GH, NY, U, and VEN and the literature on *llex* revealed that these specimens represent a new species.

With the new species described below, this genus now includes 83 species for Venezuela, 54 of which are endemic (Loizeau & Barriera, 2008); eight taxa are present in the Venezuelan Andes and only four of them (Ilex guaramacalensis Cuello & Aymard, I. kunthiana, I. myricoides Kunth, I. truxillensis var. bullatissima Cuatrecasas) are known from Venezuelan páramos. Ilex pernervata Cuatrecasas, known from Mérida state (Loizeau & Barriera, 2008), could also be present in páramo areas.

Ilex guaramacalensis Cuello & Aymard, sp. nov. TYPE: Venezuela. Trujillo: Mun. Boconó, Parque Nac. Guaramacal, bosque de 8−10 m de alto, sobre lomas adyacentes a las lagunas del Páramo El Pumar, Parcela No. 35, UTM 368063 E, 1018977 N, 2890 m, 16−17 Feb. 2005 (♀ fl., fr.), N. Cuello, W. Albarrán, L. Linares, R. Caracas, L. Zambrano y P. Tovar 2771 (holotype, PORT; isotypes, US, VEN). Figure 1.

Species proxima *Ilici kunthianae* Triana, sed differt vero: ramulis junioribus teretibus, dense trichomatibus albis strigosis obductis, foliis ellipticis vel late ellipticis, subtus sparse strigoso-pubescentibus vel pilosulis, venis utrinque 5 ad 6 paribus; inflorescentiis pistillatis 1.5–2(–3) mm longis, sparse strigoso-pubescentibus, pedicellis teretibus, floribus 4-meris, calycis lobis extus adpresse pubescentibus, petalis lobis oblongis, 1.5–2 mm longis, margine erosis.

Shrub to small tree, 2.5–10(–15) m tall; trunk 2.5–40 cm DBH, densely branched; branches sparsely strigose-pubescent, glabrous when mature; young branchlets terete, densely covered by white strigose trichomes; stipules narrowly lanceolate, acute, stiff, glabrous, 0.8–1.2 mm long, ca. 0.5 mm wide at the

base, persistent. Leaves coriaceous, glabrous, shiny adaxially, punctate and sparsely strigose-pubescent to pilosulose abaxially (the pubescence denser at the base and along midnerve), elliptic to widely elliptic, $1-3 \times 0.8-1.5$ cm, the base and apex obtuse to rounded, margin revolute and crenulate, 5 to 7 pairs of teeth, 0.2-0.3 mm, apically glandulous or slightly mucronate, 2-3 mm distant; midnerve sulcate adaxially, prominent abaxially; lateral veins in 5 to 6 pairs, anastomosing near margin, impressed adaxially, slightly elevated abaxially; tertiary venation impressed adaxially, inconspicuous abaxially; petioles (1-)2-3(-4) mm, glabrous. Staminate inflorescences solitary cymes, axillary, 1- to 3-flowered, 4-6 mm, sparsely strigose-pubescent. Pistillate inflorescences solitary cymes, axillary, 1-flowered, 1.5-2(-3) mm, floral bracteoles 2, triangular, 0.5-1 mm, strigose at the base. Flowers 4-merous; pedicels terete, sparsely strigose-pubescent, 1-2(-3) mm; calyx lobes suborbicular to rounded, obtuse, externally appressedpubescent, glabrous inside, ciliate on the margins, 1- $1.5 \times 1-2.5$ mm; corolla white, glabrous, 2-2.5(-3)mm, petals connate at the base, oblong, rounded at apex. Staminate flowers with a yellowish green conical pistillode, ca. 1 × 0.5 mm; petal lobes ca. 1.5 mm, margins entire; stamens 4, alternate with the petals, epipetalous, ca. 2 mm; anthers sagittate, yellowish purple, longitudinally dehiscent, $0.6-1 \times 0.5-$ 0.6 mm, filament white, 0.5-1 mm. Pistillate flowers with a pyriform pistil; ovary 4-carpellate, $1.5-2 \times 1$ 1.2 mm, stigma capitate, ca. 0.5 × 1.2 mm; petal lobes 1.5-2 mm, margins erose; staminodes 4, white, epipetalous, alternate to lobes, ca. 2 mm; sterile anthers flattened, sagittate. Fruit globose, yellowish green when mature, 4-5 mm diam.; mesocarp fleshy; stigma persistent, capitate; pyrenes 1 to 4 per fruit, beige to translucent, fusiform or 2-angled, the angles rounded, dorsally convex, $3-4 \times 1.5-2$ mm; seed brown, $1.8-2 \times 1-1.5$ mm.

Distribution and ecology. Ilex guaramacalensis is so far endemic to Venezuela and known only from the subpáramo, páramo, and Andean forests from 2750–3100 m on the highest reaches of the Guaramacal massif in Trujillo state. The forests where this species appears can be classified as upper montane rainforest and subalpine rainforest (UMRF, SARF, sensu Grubb, 1977) or Andean and high Andean forest (according to Cuatrecasas, 1934). The specific forest community is an association of Geissanthus andinus Mez and Miconia jahnii Pittier (Cuello & Cleef, in press). Ilex guaramacalensis is found as a relatively dominant species in the canopy layer or as an emergent tree. These forests have a low stature from 5–12 m, evergreen, with a notable litter layer, and are character-

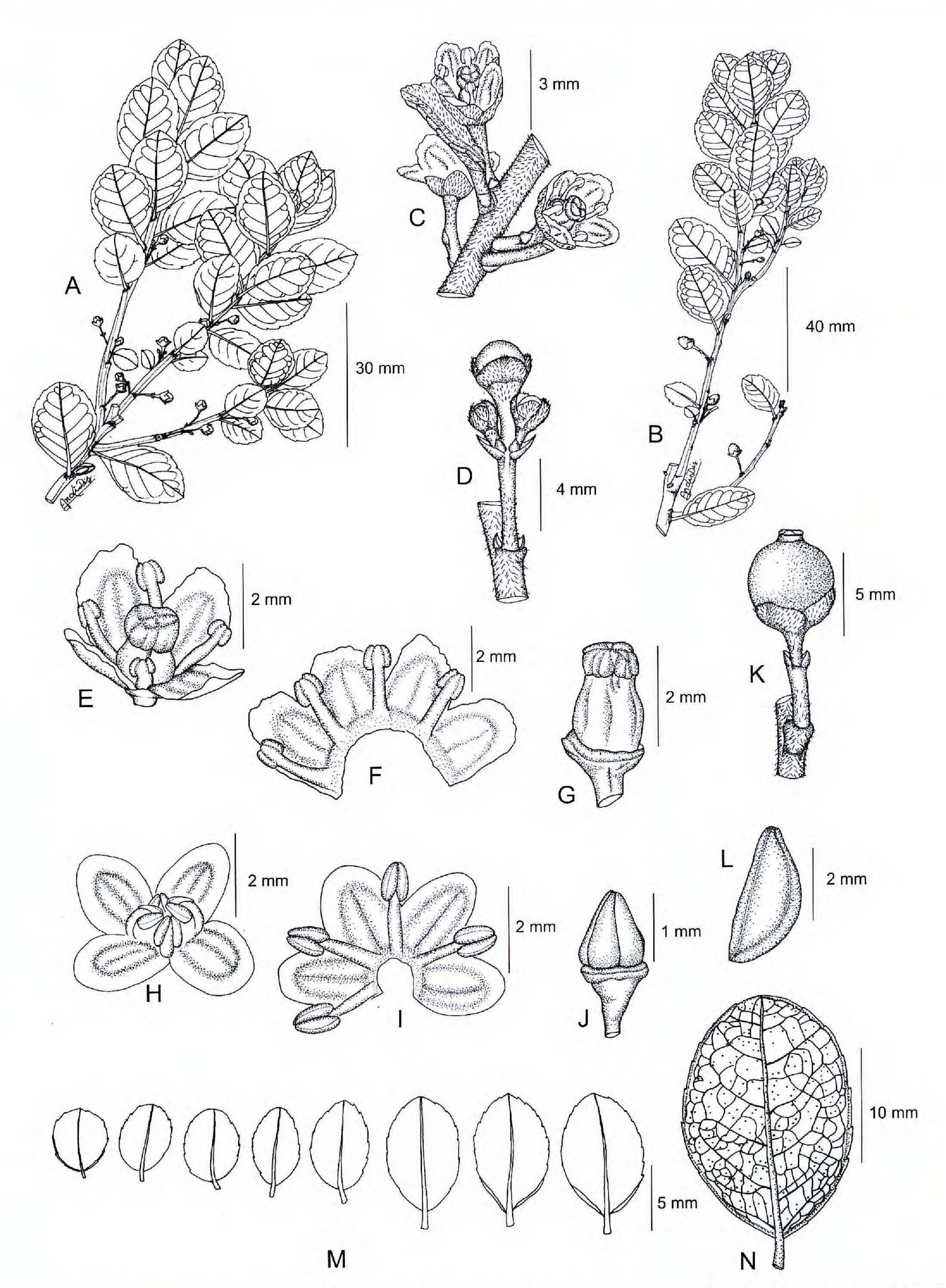


Figure 1. Ilex guaramacalensis Cuello & Aymard. —A. Staminate flowering branch. —B. Pistillate flowering branch. —C. Pistillate inflorescence showing bracts and bracteoles. —D. Staminate inflorescence bud. —E. Pistillate flower. —F. Corolla and staminodes. —G. Pistil. —H. Staminate flower. —I. Corolla and stamens. —J. Pistillode. —K. Fruit. —L. Lateral view of a pyrene. —M. Leaf shapes and sizes. —N. Detail of leaf venation. A, D, H–J, based on Cuello et al. 2701; B, based on the type Cuello et al. 2771; C, E–G, K, L, based on Cuello et al. 2942; M and N, based on Cuello et al. 2701, 2771, 2942.

ized by an almost permanent cloudiness and an extraordinary density of epiphytic mosses and liverworts. The most common tree species growing together with *I. guaramacalensis* in these forests are *Cy-bianthus marginatus* (Bentham) Pipoly, *G. andinus*, *Hesperomeles obtusifolia* (Person) Lindley, *M. jahnii*, *M. tinifolia* Naudin, *Myrsine dependens* (Ruiz & Pavón) Sprengel, *Oreopanax discolor* Decaisne & Planchon, *Symplocos tamana* Steyermark, *Vaccinium corymbodendron* Dunal, and *Weinmannia lechleriana* Engler.

Ilex guaramacalensis also appears scattered as dwarf trees in the humid shrub páramo association of Disterigma acuminatum (Kunth) Niedenzu and Arcytophyllum nitidum (Kunth) Schlechtendal (Cuello & Cleef, in prep.) growing together with other dwarf trees or shrubs up to 3 m tall such as Chaetolepis lindeniana (Naudin) Triana, Hypericum juniperinum Kunth, Palicourea jahnii Standley, and Ugni myricoides (Kunth) O. Berg; along with the stem rosettes Blechnum schomburgkii (Klotzsch) C. Christensen, Ruilopezia paltonioides (Standley) Cuatrecasas, and R. lopez-palacii (Ruiz-Terán & López-Figueiras) Cuatrecasas; the dwarf shrubs Disterigma acuminatum (Kunth) Niedenzu, D. alaternoides (Kunth) Niedenzu, Hypericum cardonae Cuatrecasas, H. paramitanum N. Robson, and Pernettya prostrata (Cavanilles) DC.; the big ground rosette Puya aristeguietae L. B. Smith; tussocks of Cortaderia hapalotricha (Pilger) Conert; and the bamboos Chusquea angustifolia (Sodestron & C. E. Calderón) L. G. Clark and Neurolepis glomerata Swallen.

It seems that in perhumid climates, *Ilex* species are common in high Andean forests and shrubby páramo. In the rainy massif of Tatamá in the Colombian Western Cordillera, at least six different *Ilex* species have been documented (Rangel et al., 2005). In the rainy massif of Guaramacal, to date, in addition to *I. guaramacalensis*, *I. myricoides* and *I. truxillensis* var. bullatissima are found in the Andean forests, while *I. laurina* Kunth and two additional undetermined species are found in the subandean forests (Dorr et al., 2000; Cuello & Cleef, in press).

IUCN Red List category. According to IUCN Red List criteria (IUCN, 2001), the new species should be included in the category Least Concern (LC) at the regional level because it is legally protected within the borders of the Guaramacal National Park and numerous individuals are frequently found in the area. According to our field data, at least 60 mature individuals of *Ilex guaramacalensis* were recorded in 0.455 ha. of surveyed upper montane forests within the area of Guaramacal National Park (Cuello & Cleef, in press).

Phenology. Ilex guaramacalensis has been collected in flower and in fruit from January to April.

Relationships. In accordance with the inflorescence classification proposed by Loizeau and Spichiger (1992), this new species belongs to the group with a solitary dichasium. By its small leaves (ca. 3 cm long), crenulate margins, lateral anastomosing nerves, and pistillate, 1-flowered inflorescences, Ilex guaramacalensis is morphologically similar to I. kunthiana from the Andes of Venezuela to Ecuador (Luteyn, 1999; Jørgensen & León-Yánez, 1999) and from the high mountains of Costa Rica and Panama (W3FM). However, I. guaramacalensis differs from I. kunthiana by its terete young branchlets densely covered by white strigose trichomes (vs. quadrangular, glabrous young branchlets); elliptic to rounded leaves that are sparsely strigose-pubescent to pilosulose abaxially (vs. leaves glabrous on both sides) and have five or six pairs of lateral veins (vs. three or four pairs); axillary pistillate inflorescences (vs. opposed pistillate inflorescences), 1.5-2 mm long (vs. 8-10 mm long), and sparsely strigose-pubescent (vs. glabrous); terete pedicel (vs. 4-angled); 4-merous flowers (vs. 5merous); externally appressed pubescent calyx lobes (vs. glabrous outside); and oblong petal lobes with erose margins, 1.5-2 mm long (vs. ovate with entire margins, 3–3.5 mm long).

Paratypes. VENEZUELA. **Trujillo:** Mun. Boconó, Parque Nac. Guaramacal, páramo de Guaramacal, alrededores de las antenas, UTM 369782 E, 1020835 N, & fl., N. Cuello, W. Albarrán, L. Linares, R. Caracas y L. Zambrano 2701 (G, MO, PORT, US, VEN), & fl./fr., N. Cuello, W. Albarrán y M. Valladares 2942 (NY, PORT, VEN); páramo "El Pumar," parcela No. 34, UTM 369585 E, 1020286 N, N. Cuello, W. Albarrán, L. Linares, R. Caracas y L. Zambrano 2683 (MER, PORT, VEN), parcela No. 36, UTM 368111 E, 1018943 N, N. Cuello, W. Albarrán, R. Caracas, P. Tovar y L. Zambrano 2798 (MERC, PORT); bosques remanentes cerca de la carretera hacia las antenas, vertiente N, parcela No. 39, UTM 369545 E, 1021382 N, & fl., N. Cuello, W. Albarrán, L. Zambrano y M. Valladares 2853 (PORT, VEN).

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Literature Cited

- Axelius, B. & W. G. D'Arcy. 1993. A new species of *Deprea* (Solanaceae) from Venezuela. Novon 3: 11–13.
- Aymard C., G., L. J. Dorr & N. Cuello. 1999. Rudgea tayloriae (Rubiaceae), an unusual new species from the eastern slopes of the Venezuelan Andes. Novon 9: 315–317.
- Carnevali, G. & I. Ramírez. 1998. Notes on the orchid flora of the Cruz Carrillo National Park (Guaramacal), Venezuela. Harvard Pap. Bot. 3(2): 239–252.
- Cuatrecasas, J. 1934. Observaciones geobotánicas en Colombia. Trab. Mus. Nac. Ci. Nat., Ser. Bot. 27: 1–144.
- Cuello, N. (editor). 1999. Parque Nacional Guaramacal. UNELLEZ-Fundación Polar, Caracas.
- Parque Nacional Cruz Carrillo en los Andes de Venezuela. Pp. 127–130 in Memorias del IV Congreso Latinoamericano de Ecología: Ecología y Desarrollo Sostenible: Reto de America Latina para el Tercer Milenio. Arequipa, Perú.
- ———. 2002. Altitudinal changes in forest diversity and composition in the Ramal de Guaramacal in the Venezuelan Andes. Ecotropicos 15(2): 160–176.
- ——— & A. M. Cleef. The forest vegetation of Ramal de Guaramacal in the Venezuelan Andes. Phytocoenologia (in press).
- Dorr, L., B. Stergios, A. Smith & N. Cuello. 2000. Catalogue of the Vascular Plants of Guaramacal National Park, Portuguesa and Trujillo States, Venezuela. Contr. U.S. Natl. Herb. 40.
- Edwin, G. 1965. Aquifoliaceae. *In* B. Maguire et al. (editors), The Botany of Guayana Highland. Part VI: Studies in Mexican Compositae. I. Miscellaneous New Species. Mem. New York Bot. Gard. 12(3): 124–150.
- ——. 1967 [1968]. Part VI. Family 102. Aquifoliaceae. *In* R. E. Woodson Jr. & R. W. Schery (editors), Flora of Panama. Ann. Missouri Bot. Gard. 75: 381–387.
- Galle, T. C. 1997. Hollies: The Genus *Ilex*. Timber Press, Portland.
- Giberti, G. C. 1979. Las especies Argentinas del género *llex* L. (Aquifoliaceae). Darwiniana 22: 217–240.
- ————. 1994. Aquifoliaceae. Pp. 1–34 in R. Spichiger & L. Ramela (editors), Flora de Paraguay, Vol. 24. Conservatoire et Jardin Botaniques de la Ville de Genève, Geneva.
- González-Gutiérrez, P. A. & J. Sierra-Calzado. 2004. Aquifoliaceae. *In* W. Greuter & R. Rankin-Rodríguez (editors), Flora de la República de Cuba. Ser. A, Plantas Vasculares, Fasc. 9(1). Koeltz Scientific Books, Königstein.
- Gray, A. 1856. A Manual of the Botany of the Northern United States, ed. 2. Putnam & Co., New York.

- Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. Ann. Rev. Ecol. Syst. 8: 83–107.
- Hahn, W. L. 1993. A synopsis of the Panamanian species of *Ilex* (Aquifoliaceae). Novon 3: 34–45.
- ———. 2001. Aquifoliaceae. *In* W. D. Stevens, C. Ulloa U., A. Pool & O. M. Montiel (editors), Flora de Nicaragua. Angiospermas: Acanthaceae–Euphorbiaceae. Monogr. Syst. Bot. Missouri Bot. Gard. 85(1): 133–136.
- Hu, S. Y. 1949. The genus *Ilex* in China. J. Arnold Arbor. 30: 233–344.
- _______. 1950. The genus *Ilex* in China. J. Arnold Arbor. 31: 39–80.
- IUCN. 2001. IUCN Red List Categories and Criteria Version 3.1. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- Jørgensen, P. M. & S. León-Yánez (editors). 1999. Catalogue of the Vascular Plants of Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 75.
- Loesener, T. 1901. Monographia Aquifoliacearum, Pars I. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 78: 1–567.
- ————. 1908. Monographia Aquifoliacearum, Pars II. Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 89: 5–314.
 ———. 1942. Aquifoliaceae. Pp. 36–86 in A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 20b, 2nd ed. Wilhelm Engelmann, Leipzig.
- Loizeau, P. A. 1994. Les Aquifoliaceae péruviennes (eléments pour une révision des Aquifoliaceae néotropicales). Boissiera 48: 1–306.
- ——— & R. Spichiger. 1992. Proposition d'une classification des inflorescences d'*Ilex* L. (Aquifoliaceae). Candollea 47: 99–112.
- ——— & G. Barriera. 2008. Aquifoliaceae. Pp. 213–215 in O. Hokche, P. Berry & O. Huber (editors), Nuevo Catálogo de la Flora de Venezuela. Fundación Instituto Botánico de Venezuela, Caracas (in press).
- Towards an understanding of the distribution of *Ilex* L. (Aquifoliaceae) on a world-wide scale. Biol. Skr. 55: 501–518.
- ———, V. Savolainen, S. Andrews & R. Spichiger. 2007. Aquifoliaceae. *In* K. Kubitzki (editor), The Families and Genera of Vascular Plants. Springer-Verlag, Berlin.
- Luteyn, J. 1999. Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. Mem. New York Bot. Gard. 84.
- Morillo, G. 1988. Nuevas especies de Asclepiadaceae para Venezuela. Ernstia 34: 12–30.
- Niño, M., L. Dorr & F. W. Stauffer. 2005. Una nueva especie de *Aiphanes* (Arecaceae) de la Cordillera de Mérida, Venezuela. Sida 21: 1529–1606.
- Ortega, F., G. Aymard & B. Stergios. 1987. Aproximación al conocimiento de la Flora de las Montañas de Guaramacal, Edo. Trujillo, Venezuela. BioLlania 5: 1–60.
- Rangel Ch., J. O., O. Rivera D., P. Franco-R., J. H. Torres, T. van der Hammen & A. M. Cleef. 2005. Catálogo de la flora vascular del macizo de Tatamá. Pp. 287–376 in T. van der Hammen, J. O. Rangel & A. M. Cleef (editors), La Cordillera Occidental Colombiana, Transecto Tatamá. Estudios de Ecosistemas Tropandinos 6. J. Cramer, Berlin, Stuttgart.
- Stančik, D. 2004. Festuca dinirica and F. guaramacalana (Poaceae, Loliinae), two new species from the Venezuelan Andes. Novon 14: 341–344.
- Stergios, B. & L. Dorr. 2003. Bomarea amilcariana (Amarylidaceae). Acta Bot. Venez. 26: 31–40.

- Steyermark, J. A. 1988. Aquifoliaceae. *In* Flora of the Venezuelan Guayana–IV. Ann. Missouri Bot. Gard. 75: 320–333.
- —— & P. E. Berry. 1995. Aquifoliaceae. Pp. 571–599 in J. A. Steyermark, P. E. Berry & B. K. Holst (editors), Flora of the Venezuelan Guayana, Vol. 2. Timber Press, Portland, and Missouri Botanical Garden Press, St. Louis.
- Taylor, C. 2002. Rubiacearum Americanarum Magna Hama Pars X. New species and a new subspecies of *Faramea* (Coussareae) from Central and South America. Novon 12: 563–570.
- W³FM. Flora Mesoamericana Home Page and Checklist. http://www.mobot.org/MOBOT/fm, accessed 30 May 2008.